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Zygophlebia, a New Genus of Grammitidaceae

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In my studies for the generic realignment of the Neotropical, anhydathodous Grammitidaceae, it has become clear that there is a small group of paraphysis-bearing species that is quite distinct from *Ceradenia* (Bishop, 1988). This assemblage includes seven American species and one or more from Africa. Of the American species two are fairly common and widespread, three are rare and localized, and two are new. Surprisingly, there has never been a suggestion of the interrelationship of any of the described species, but the continuity of these taxa now seems obvious. The decision to erect a new genus, instead of including these species in *Ceradenia* as subgenus, has required careful consideration. In addition to the correlated morphological and anatomical characters, an important factor has been that the ease of identification and mutual hierarchic integrity of the related genera would be undermined by the inclusion of these species in a single genus.

Zygophlebia is named for the strong tendency for the fronds to show areolate venation. Regular anastamoses are present in four species, in the others they are irregular to a varying extent. Anastamosing veins are uncommon in the Grammitidaceae, and at least in the New World, *Zygophlebia* is the only genus with pinnate or pectinate-pinnatifid species that have regularly anastamosing veins (Fig. 3C). The most densely areolate species is *Z. cornuta* in which the fertile veinlets are usually prolonged beyond the sorus to form costal areolae and the sterile veinlets are once or twice forked and form an irregular reticulum or at least a series of distal areolae. The clearly related *Z. sectifrons* shows generally regular costal areolae with free or irregularly connivent sterile veins. *Zygophlebia mathewsii* and *Z. werffii* exhibit a fairly regular intramarginal vein formed by the fusion of the sterile veinlets. The fertile veinlets are only irregularly prolonged and fused with the next distal sterile veinlet. The largest plants of *Z. longipilosa* exhibit a similar venation pattern, but the smaller plants show only irregular fusion of the sterile veinlets, as is the case of the smallest plants of *Z. mathewsii*. The species with veins most regularly free are *Z. dudleyi* and *Z. eminens*. However, in these the sterile veinlets are often forked and irregular, and marginal fusion is not uncommon.

Irregular anastamoses are seen in various species of *Ceradenia* subg. *Filicipecten*. The most common type involves the connivence of a shortly prolonged fertile veinlet with the sterile fork of the same vein. Costal areolation formed by the fertile veinlet's fusion with the next distal sterile veinlet or the marginal connivence of sterile veinlets is quite rare. Except at the very base of the pinnae of certain species, even the sterile veinlets are rarely forked distally.

It is of note that *Z. werffii* and large examples of *Z. longipilosa*, both usually with intramarginal veins, are smaller than larger examples of *Ceradenia*, so that the argument that areolation in these ferns is a direct response to larger size is vitiated. It does seem clear that in *Zygophlebia* itself relatively free vein patterns

are generally correlated with smaller frond size. The pattern of irregular anastomoses in *Zygophlebia* species with mostly free veins to me strongly suggests their derivation from a larger, areolate ancestor. On the other hand, the lack of a similar venation pattern in even the largest species of *Ceradenia* seems to point to an ancestral stock with free veins.

Few contemporary pteridologists would recognize genera based solely on venation. The clearest difference between *Zygophlebia* and *Ceradenia* is found in the paraphyses. Morphologically, these are similar in both genera. They consist of a uniseriate stalk, the terminal cell of which bears two glands distally. Some species of *Zygophlebia* have only these two glands; others bear a third distolaterally from the subterminal stalk cell. *Ceradenia* species have paraphyses with 1–4 subterminal cells bearing glands. The lowest of these glands may be supported by a stalk cell. Paraphyses of each genus protect the developing sporangia and may be considered functionally mature at the time the capsules are exserted between them. At this time the paraphyses of *Zygophlebia* are brown and thickly viscid, so that in dried specimens at least, the entire sorus adheres into a single sticky mass. Microscopically, the brown glands never show an external accumulation at any stage. In *Ceradenia* the paraphyses are waxy white, yellowish, tan, or red (unless colorized by specimen preparation) and show no tendency to adhere to each other or to the sporangia. The appearance of the glands microscopically is striking. Each is overlain by colorless, rough-textured excretion. This substance is insoluble in water, insoluble or weakly soluble in ethanol, and quickly dissolved by xylene. The positive affinity for osmic acid stain suggests a composition of long-chained fatty acids. This accumulation is still quite evident even when the color is changed by specimen preparation.

Another striking, if recondite, difference between these genera is found in the rhizome. In both the stele is siphonostelic, but in *Zygophlebia* there are ventrolateral perforations not associated with the leaf traces (Fig. 1). I have seen such gaps in *Z. mathewsii*, *Z. villosissima*, *Z. sectifrons*, *Z. cornuta*, *Z. dudleyi*, and *Z. werffii*. Material for sectioning has not been available for *Z. longipilosa* and *Z. eminens*, but their close relationship to other species makes it unlikely that either would be aberrant in this respect. No species of *Ceradenia*, of either subgenus, is known to exhibit such accessory stelar perforations.

Two additional characters common to all *Zygophlebia* species merit note. Simple or branched hairs with terminal, ultimately sticky-viscid glands occur in all species on the lamina and usually on the stipe as well. In *Z. mathewsii* and its relatives these are usually branched and spreading from the surface of attachment. In the *Z. sectifrons* group the hairs, especially on the laminar surface, are generally simple and appressed. As the frond matures they become adherent to the surface. In the most extreme case, that of *Z. sectifrons*, the hairs on mature fronds appear as dark, scarcely differentiated 'squamulae' whose morphology is scarcely discernible. In *Z. werffii* the marginal and ventral laminar hairs are mostly branched and spreading (Fig. 3C), whereas those of the dorsal surface are simple and appressed.

The rhizomes of all species support the stipes on distinct, bulbous

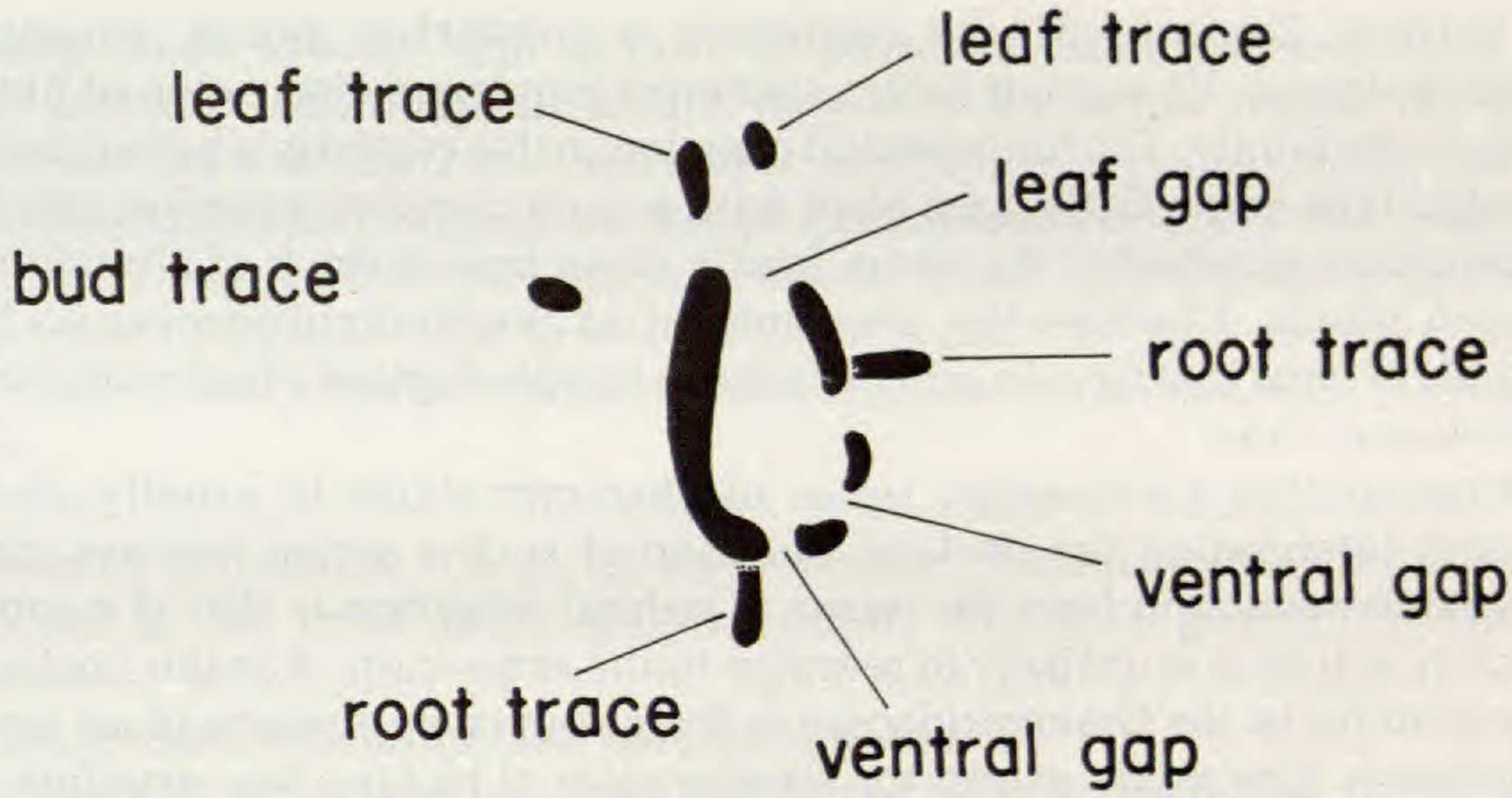

FIG. 1. *Zygophlebia sectifrons*. Diagram of stelar cross section.

phyllopodia. Most larger members of the family have phyllopodia of some sort, but they have been little discussed. In *Zygophlebia* they are well developed. The cortical tissue of which they are composed is usually distinctly darker (dark brown or blackish) than the stipe. A bud is conspicuously visible at the stipe base of younger fronds as a whitish, parenchymatous mass on the exteriolateral side of the phyllopodium. This structure is scarcely noticeable in older fronds unless developed as a branch. The abscission layer is clearly functional. The fallen stipe leaves a shallowly concave scar normally surrounded by an annular thickening.

The eight species of *Zygophlebia* fall into three distinct groups. *Zygophlebia mathewsii*, *Z. longipilosa*, and *Z. villosissima* all have laminar setae, which the other species lack, and all three show fundamentally distal soriation. The sori never extend to the rachis and they usually reach the tips of the pinnae (occasional specimens of *Z. mathewsii* may have sterile segment tips). The *Z. sectifrons* group also includes *Z. cornuta*, *Z. eminens*, and *Z. dudleyi*. These four epiphytic species completely lack laminar setae and their soriation is essentially basal. The sori often reach the rachis and the segments show a sterile apical portion. Among these species *Z. eminens* and *Z. dudleyi* appear closely related by virtue of their smaller, paler scales and the presence of scattered, long setae along the dorsal rachis. *Zygophlebia sectifrons* and *Z. cornuta* have long, relatively narrow, medium brown scales, areolate venation, and lack setae on the rachis (except in occasional specimens of *Z. sectifrons*). *Zygophlebia werffii* stands apart from the rest. It is terrestrial and nearly pinnate, with ciliate scales, blackish stipes, erect, unflexed fronds, and numerous, short setae on the rachis. Like the species of the *Z. sectifrons* group, the pinnae lack setae and the soriation is basal, so that the relationship of *Z. werffii* may be closer here than to the *Z. mathewsii* group. Although these groups are quite distinct, because of the few species involved, it seems unnecessary to recognize them formally as infrageneric taxa.

I believe *Zygophlebia* to represent a primitive genus among the Grammitidaceae. To support such a statement requires a discussion of phyletic trends in the family. The fundamental question in this regard is whether the most ancestral type was a fairly large plant with a more complex venation and stelar organization, or whether the entire family arose from a stock of already much reduced plants. I believe the development of the Grammitidaceae to be an example of ferns that have in general become morphologically less complex over evolutionary time.

Demonstrating a sequential series of character states is usually straightforward; interpreting the phyletic direction of such a series requires care. A reasonable deduction from the tenets of natural selection is that if a complex structure is lost, it is unlikely to reevolve in the same form. A major anatomical discontinuity in the Grammitidaceae is the presence or absence of an internal endodermis. One might expect the simpler state of lacking this structure to be associated with smaller rhizomes. However, many small species show the more complex organization (e.g., *Cochlidium*, *Lomaphlebia*, many southeast Asian species of *Grammitis* sensu Parris, 1983), whereas *Adenophorus*, which has some rather large species (*A. tamariscinus*, *A. tripinnatifidus*, *A. periens*), lacks an internal endodermis, as do some large Neotropical species such as *G. semihirsuta*. These observations suggest that once lost, the internal endodermis is not subsequently redeveloped even in a phyletic line becoming larger in rhizome size.

Accessory stelar perforations are found at least in *Zygophlebia*, *Ctenopteris*, and *Lomaphlebia*, all of which show an internal endodermis. Although the argument in this case is admittedly tentative, considering the previous discussion of these perforations in connection with *Zygophlebia* and *Ceradenia*, it seems likely that these are more easily lost in phyletic lines showing size reductions than they are apt to be developed *de novo* with increased size.

The ancestral frond pattern in the Grammitidaceae was probably pectinate. The genus *Enterosora* provides an illuminating situation in this regard. Although closely related to *Zygophlebia* and *Ceradenia*, most of the species have more or less simple fronds. The largest species (e.g., *E. trifurcata* (L). comb. ined.) do have deeply lobed, pinnatifid fronds, but the lobes here are very broad and mostly rounded, not at all like the pectinate laminae found throughout *Zygophlebia* and *Ceradenia* subg. *Filicipecten*. This suggests that pinnatifid laminae in *Enterosora* have derived from simple fronds and that pectinate fronds to not directly result from such a derivation.

A dorsiventral rhizome probably represents the more primitive condition in the family relative to the radially symmetrical rhizome. Except for debris-collecting epiphytes such as the *Asplenium nidus* group, it is reasonable that a creeping, dorsiventrally organized rhizome is functionally adaptive for all but very reduced epiphytes. Most Grammitidaceae with radially symmetrical rhizomes, such as *Grammitis* sensu stricto and *Cochlidium*, are quite small. *Ceradenia* subg. *Ceradenia*, also with such a rhizome, includes some rather large species, but, as I will discuss elsewhere, I believe the ancestral stock of that subgenus was probably a small species, such as *C. jungermannioides* or *C. pruinosa*.

Among those species with pinnate or pinnatifid fronds, forked veins are almost certainly primitive. In groups in which the fertile veinlet has been suppressed (such as the *G. cultrata* and *G. moniliformis* groups), larger species do not develop forked veins, even though careful examination of the veins will often clearly suggest their derivation from a more elaborate arrangement. I have posited that in *Zygophlebia*, areolate veins represent the more primitive state, and I think it likely that the ancestral Grammitidaceae also had such a venation pattern.

Whether the presence of hydathodes is ancestral or derived can best be supposed by correlation. The putatively primitive character states just discussed are found in the three large, anhydathodous American genera (*Ceradenia*, *Zygophlebia*, Enterosora). On the other hand, most of the derived states are more common in the Grammitidaceae with hydathodes.

In summary, the primitive Grammitidaceae were probably relatively large ferns with pectinate, anhydathodous fronds, areolate or at least forked veins, and a dorsiventral rhizome with an internal endodermis and accessory stelar perforations. In other words, they were very much like some species of *Zygophlebia*, and I take this genus to be the most primitive extant example of the family. Unless otherwise noted, I have examined all specimens cited. Loans were obtained from AAU, B, BM, C, F, GH, K, MO, NY, P, S, and US, and I thank the curators for making these specimens available. Full specimen citations for *Z. mathewsii* and *Z. sectifrons* are available on request.

Zygophlebia L. E. Bishop, gen. nov.—TYPE: *Polypodium sectifrons* Kunze ex Mett.

Hinc contraho circulum specierum majorum quarum cognatio inter se ad nunc non percipiebatur. Rhizoma est validum dorsiventrale phyllopodios bene effectos ferens interne siphonostelam amphiphloicam cum endoderme interna et perforationibus accessoriis ventrolateralibus, externe paleas concolores nitentes vel subnitentes in margine glandulis unicellularibus et per unam speciem ciliis praeditas ostendit. Lamina profunde pinnatifida vel perpinnata (una specie) cum aut sine setis, pilos glandulares simplices vel ramosos gerens, venis 1–2(3)-furcatis nunc regulatim conniventibus nunc plusminusve liberis, hydathodis caret. Sori submediales vel mediales ad venulam acroscopicam siti, setis circumsoralibus in 2 speciebus invenitis, sporangia capsulis 195–320 × 155–265 μm harum annuli ex 12–18 cellulis constantes, sporas hemisphaericas vel subtetraedricas aliquando binucleatas 28–60 μm in diametro longiore includentibus, necnon paraphyses quae gerrent distaliter 2–3 glandulas brunneas viscidas autem his strata externa exsudati solidi ceracei microscopio visibili carentibus, comprehendent.

KEY TO THE NEOTROPICAL SPECIES

1. Lamina setose; sori usually distal on the segments, not extending to the rachis.
   2. Rhizome scales dark, lustrous brown; setae scattered over the dorsal lamina (Costa Rica, Panama, Andes) . . . . . 1. *Z. mathewsii*

2. Rhizome scales (at least the younger ones) tan or light brown; setae on the dorsal lamina localized on the costa and around the sorus (Brazil) . . . . . 2. *Z. longipilosa*

1. Lamina without setae (unless near rachis); sori basal, often reaching the rachis, but not extending to the segment tips.
3. Rhizome scales ciliate; stipe blackish; rachis with numerous, short setae; fronds erect, unflexed (Peru) . . . . . 7. *Z. werffii*
3. Rhizome scales eciliate, though often with marginal glands; stipe brown; rachis with a few, scattered, long setae or none; fronds mostly pendent and flexed at lamina base.
4. Rhizome scales medium brown, up to more than 10 mm; rachis usually without scattered setae dorsally.
5. Pinnae linear-elongate, set at 20–60° angle to the rachis, separated by 1–5 times their width (Caribbean, Costa Rica, Panama, Venezuela, Colombia) . . . . . 3. *Z. sectifrons*
5. Pinnae linear-triangular, set at 70–90° angle to the rachis, separated by 0.5–1.5 times their width (Costa Rica, Panama) . . . . 4. *Z. cornuta*
4. Rhizome scales tannish brown, usually less than 8 mm long; rachis with scattered setae dorsally.
6. Stipe with few, scattered setae; pinnae approximate, separated by less than their width (Ecuador) . . . . . 5. *Z. eminens*
6. Stipe densely setose in proximal half; pinnae distant, separated by at least their width (Peru) . . . . . 6. *Z. dudleyi*

1. **Zygophlebia mathewsii** (Kunze ex Mett.) L. E. Bishop, comb. nov. ← *Polypodium mathewsii* Kunze ex Mett., Abh. Senckenberg. Naturf. Ges. 2:74. 1856.—*Grammitis mathewsii* (Kunze ex Mett.) C. Morton, Amer. Fern J. 60:66. 1970.—TYPE: "Peru (Mathew)." There are three Mathews' sheets at B. One is a frond of a larger plant with a questioned collection number (*3281*) which is not duplicated at other herbaria. The two other sheets bear the number 1811 and represent a smaller expression of the species. Of these I select the sheet from Mettenius' herbarium as lectotype. Other isolectotypes are at BM, K, P.

Goniophlebium villeminianum Fée, Mém. foug. 7:63, t.27, f.3. 1857.—TYPE: [Colombia] "Habitat in Ocaña Nova-Granatensium (Paramos). Altitud. 3400–3700 metr.," *L. Schlim 1009* (RB not seen; Windisch, 1982).

A medium to large species, primarily epiphytic but occasionally lithophytic, or terrestrial in páramos; rhizome usually quite stout, with dark brown, shining scales up to 10 × 1.2 mm, with obovate, marginal cells when young; stipe brown, regularly flexed toward apex, 8–30 cm × 0.7–2.0 mm, variously provided throughout its length with castaneous to dark brown setae up to 5 mm long and simple or branched glandular hairs; rachis prominently protruding dorsally, ventrally prominulous or in same plane as lamina, brown or covered with lamina tissue, with hairs and setae usually not much differentiated from those of the lamina; lamina coriaceous, mostly linear-elliptic or narrowly lanceolate, deeply pinnatifid, 10–50 × 2–13 cm, narrowed through 1—several

pairs of basal pinnae, the tip (rarely present in specimens) prolonged into an apical segment; pinnae to 75 × 3–8 mm, at times subapproximate with narrowly acute sinuses but mostly separated by 1–3 times their width and with broadly angled or rounded sinuses, mostly set at 70–90° to the rachis but occasionally more sharply angled, linear, linear-oblong, or linear-triangular, straight or variously falcate, at base basiscopically widened or decurrent, acroscopically straight to surcurrent, apically acuminate, shortly acute, or broadly rounded, margin distinctly to strongly revolute, costa prominulous on either side or occasionally immersed ventrally, setae usually distributed evenly over dorsal surface, less densely so ventrally, and at times differentiated (darker, denser, and/or longer) on margin, dorsal costa, and around sori, glandular hairs very variable in their size, distribution, and abundance on dorsal surface and margin; venation mostly areolate with the distal fusion of the sterile veinlets, with the fertile veinlet terminated by the sorus or prolonged and variously connivent, at times the areolation very irregular; stomata 55–80 × 50–63 μm; sori superficial, usually slightly inframedial but often appearing medial due to the revolute margin, up to 27 pairs per pinna, not reaching the rachis and often clearly distal but at times absent from a sterile pinna apex, occasionally attended by differentiated circumsoral setae; capsules 240–320 × 200–265 μm, with 13–16 annulus cells, the distal ones 40–50 μm high; spores 50–60 μm in longer diameter.

Distribution. Costa Rica, Panama, Colombia to Bolivia. Elevation (800) 1800–3200 m.

With rare occurrences in Panama and Costa Rica, this is primarily a species of the Andes, where it is apparently rather common in cloud forests at higher elevations. The Bolivian collection from 800 m in the Corani Valley should be questioned. But it must be pointed out that the Corani Valley is very deep and steep-sided, extending up rapidly into the normal habitat of this species. Therefore, if the label is accurate with respect to elevation, a spore or even plant source would be available within a short, lateral distance of the locality.

This species is remarkably variable with respect to size, shape, and placement of the pinnae and to details of the indument, but I have been unable to correlate any character variation with geography. The very large sporangia and spores of *Z. mathewsii* compared to those of its relatives suggest a polyploid condition and indicate the desirability of chromosome counts.

2. **Zygophlebia longipilosa** (C. Chr.) L. E. Bishop, comb. nov.—*Polypodium villosum* Fée, Crypt. vasc. Brésil 2:54, t.95, f.3. 1873, *non* L. *nec* Karsten.—*Polypodium longipilosa* C. Chr., Bot. Tidsskr. 25:78. 1903, nom. nov.—TYPE: Brazil, Rio de Janeiro, Source du Rio Soberbo en haut des Orgues, *Glaziou 4411* (P). There are two sheets at P. I consider the holotype the one with a label in Fée's hand. The other, with a Glaziou label, is an isotype.

Ctenopteris subcrassa Copel., Philipp. J. Sci. 84:468. 1955 (1956).—*Grammitis subcrassa* (Copel.) C. Morton, Contr. U.S. Natl. Herb. 38:234. 1973.—TYPE: Brazil, São Paulo, Serra do Mar, Campo Grande, 800 m, *Brade 5833* (US).

Polypodium luederswaldii Rosenstock in sched. (*Lüderwald s.n.* in 1910) ex Copel. (as *P. luederswaltii*), Philipp. J. Sci. 84:468. 1955 (1956), nom. nud.

Epiphyte of moderate size; rhizome rather stout, with tan or light brown scales up to 8 × 0.5 mm; stipe brown, usually flexed toward the apex, 2–10 cm × 0.5–1.2 mm, well provided through its length with castaneous or brown setae 2–4 mm long and with much shorter, usually branched, clavate hairs; rachis clearly prominulous, mostly embedded in laminar tissue or with its sclerenchyma exposed at the base of the largest fronds, with somewhat scattered setae associated with it on both sides; lamina thinnish or subcoriaceous, linear-elliptic, linear-oblong, to narrowly lanceolate, deeply pinnatifid to within 1–3 mm of the rachis, 6–25 × 1.5–5 cm, somewhat narrowed through 2–5 pairs of basal pinnae, at the tip rounded or shortly prolonged into a terminal segment; pinnae 5–25 × 3–6 mm, mostly approximate or rarely separated by as much as their width, set at 70–90° to the rachis, generally oblong but occasionally narrowed toward the base, apically mostly rounded though at times broadly acute, with many spreading setae on the margin, with the laminar setae most conspicuously clustered around the sori, otherwise scattered along the lightly prominulous costa of either side, on the ventral surface, and uncommonly on the dorsal surface, also provided with branched clavate, possibly secretory hairs, these best developed on the margins and in varying abundance in a reduced form on the lamina surfaces; venation variable, at times almost totally free, at others completely areolate with the proximal veinlets forming an intramarginal vein and the fertile veinlet either joined with this, joined with the next distal sterile veinlet, or free; stomata 50–60 × 45–58 μm; sori superficial, medial, up to 12 pairs per segment, often clearly distal and never reaching the pinna base, prominently attended by the circumsoral setae; capsules 195–210 × 155–165 μm, with 15–17 annulus cells, the distal ones 27–32 μm high; spores 28–36 μm in longer diameter.

Additional collections: BRAZIL: **Rio de Janeiro:** Theresopolis, Serra Cavallo, *Brade 9992* (NY, UC); Frade de Macahé, 1000 m, *Brade 15806* (BM). **Santa Catarina:** Fachinal [Faxinal], Cambajuva [Bom Jardim da Serra], São Joaquim, 1200 m, *Reitz 3473* (US). **São Paulo:** *Lüderwalt s.n.* in 1910 (US); Serra do Mar, 1000 m, *Wacket s.n.* (US).

This epiphytic species is known only from three coastal states in southeastern Brazil. It is clearly rare, probably more so today than formerly, for it has been recorded only at rather low elevations (800–1200 m) and its range includes the most densely populated and utilized area of Brazil. The last gathering was in Santa Catarina in 1950.

3. **Zygophlebia sectifrons** (Kunze ex Mett.) L. E. Bishop, comb. nov.—*Polypodium sectifrons* Kunze ex Mett., Abh. Senckenberg. Naturf. Ges. 2:99, t.2, f.3–4. 1856.—*Grammitis sectifrons* (Kunze ex Mett.) F. Seymour, Phytologia 31:180. 1975.—TYPE: Based on two syntypes, *Schwanecke s.n.* from Puerto Rico and *Breutel s.n.* from St. Kitts. The Kunze sheets at LZ are destroyed and Dr. Zimmer's kind efforts to locate a sheet of Mettenius at Berlin have been unsuccessful. Therefore Proctor's lectotypification (Ferns Jamaica 585. 1985) based on a Schwanecke sheet at GH may stand. I have been able to examine a xerocopy of this sheet due to the courtesy of Dr. Rolla Tryon.

Drynaria elastica Fée, Mém. foug. 11:72, t.20, f.2. 1866.—*Polypodium petrifolium* Jenman, as "*petrafolium*," Bull. Bot. Dept., n.s. 4:139. 1897, nom. nov., non *P. elasticum* Bory ex Willd.—TYPE: Guadeloupe. Habitat in littore occidentali (Matouba, rade de Saint-Louis, Bois-David, etc.), *l'Herminier s.n.* (P). Unnumbered sheets at F, MO, NY are possible isotypes. Another l'Herminier sheet at NY bears the number 144. Because the type collection evidently included plants from more than one locality, it seems unwise to assign isotype status to any of these specimens.

A medium to large species, apparently strictly epiphytic; rhizome usually stout, with scales up to 15 × 1 mm; stipe brown, normally flexed distally, shorter than the lamina, 5–30 cm × 0.5–2.0 mm near the base, distinctly tapering distally, usually provided with dark brown setae up to 5 mm long toward the base, these more scattered or absent distally, with scattered, appressed, glandular-viscid hairs when young, these obscure at maturity; rachis prominently protruding dorsally, ventrally flat or prominulous, mostly embedded in laminar tissue, at times with scattered setae toward base dorsally, these rarely extending the entire rachis length; lamina coriaceous or subcoriaceous, ovate or oblong, deeply pinnatifid to within 1–2 mm of the prominently winged rachis, 10–35 × 5–20 cm, the lower pinnae somewhat reduced or not, the tip a distinct apical segment, this often prolonged; pinnae to 25 cm long, usually rather irregular in length, 2.5–8.0 mm wide, separated by 1–5 times their width, set at 20–60° to the rachis, linear, entire or irregularly sinuate through expansion around the sori, straight or at times falcate, often a bit narrowed near the base, basiscopically decurrent, acroscopically surcurrent, usually narrowed toward the acute to broadly rounded tip, margin flat or slightly revolute, costa prominulous dorsally, slightly prominulous to immersed ventrally, with appressed, glandular hairs scattered over either surface when young, these darkening and appearing as fairly undifferentiated, dark dots at maturity; venation irregularly areolate, the fertile veinlets usually prolonged to form costal areolae, the sterile veinlets free or forming an intramarginal vein; stomata 52–60 × 46–55 μm; sori moderately immersed, medial, often rather elongate, normally irregularly distributed, fundamentally basal, often reaching the pinna base but regularly absent from a sterile apical portion; paraphyses each usually bearing 2 glands, these clavate or broadly ellipticoid; capsules 240–280 × 140–180 μm with 12–14 annulus cells, the distal ones 35–42 μm high; spores 40–52 μm in longer diameter.

Distribution. Jamaica, Puerto Rico, Hispaniola, Lesser Antilles, Costa Rica, Panama, Venezuela, Colombia. The elevational range is rather wide but the plant seems most common, at least continentally, at 1000–2000 m. The highest certain record is 2200 m and of the five records below 1000 m (all Caribbean), the lowest is 680.

Zygophlebia sectifrons is a strikingly distinctive species, and most collectors working where it occurs soon come to recognize it. The comparatively few, distally directed pinnae of somewhat irregular length are visually characteristic. And the large, often elongate, rather irregularly disposed sori are unique to this species.

Although distinctive, *Z. sectifrons* seems clearly related to the next three

species. All have fundamentally basal soriation, no laminar setae, impressed sori, and laminar hairs that are appessed, glandular-viscid, and that darken to become structurally obscure when older. The present species appears closest to *Z. cornuta*, sharing the usual lack of setae on the rachis and similar rhizome paleae. That this latter species is of quite different superficial appearance makes their identification easy.

4. **Zygophlebia cornuta** (Lellinger) L. E. Bishop, comb. nov.—*Grammitis cornuta* Lellinger, Proc. Biol. Soc. Wash. 98:381, f. 12. 1985.—TYPE: Costa Rica, Pcia. San José, Las Nubes, ca. 1500–1900 m, *Standley 38843* (US). According to Lellinger there should be an isotype at GH.

Medium-sized epiphyte; rhizome stout, with brown, shining, linear or linear-triangular scales up to 12 × 1 mm, entire and without appended marginal cells, fronds not or but lightly flexed at lamina base, at least at times erect; stipe brown, usually as long as or longer than the lamina, 7–30 cm × 0.8–2.0 mm, usually sparsely setiferous toward the base, with the setae brown, up to 2.5 mm, through most of the stipe length with numerous, short, simple, glandular hairs, these often maintaining their visible structure at frond maturity; rachis lacking setae, prominulous dorsally, sunken ventrally, mostly embedded in the laminar tissue, the sclerenchyma sheath sometimes visible through this tissue dorsally or even exposed ventrally; lamina subcoriaceous, oblong or ovate, deeply pinnatifid to within 1–2 mm of the rachis, 7–24 × 4–10 cm, the lowest pinna-pair somewhat or not at all reduced, the tip prolonged into an apical segment; pinnae to 9 cm long, 5–9 mm wide, separated by 0.5–1.5 times their width, set at 70–90° to the rachis, linear-triangular, straight or moderately falcate, at times slightly narrowed above the decurrent and surcurrent base, gradually reduced distally to the narrowly rounded tip, margin flat or slightly revolute, the costa prominulous dorsally, ventrally immersed, with small, appressed, glandular hairs scattered mostly over the dorsal surface, at frond maturity these generally of obscure structure; venation regularly areolate, the fertile veinlets normally forming costal areolae, the sterile veinlets 2–3 times forked to form varying patterns of distal areolae; stomata 60–72 × 50–60 μm; sori subimmersed, inframedial, up to 12 pairs per segment, fundamentally basal in distribution, often reaching the rachis but regularly absent from a distal sterile cauda; paraphyses each with 2–3 (rarely 4) elongate-clavate glands; capsules 260–300 × 225–260 μm with 12–14 annulus cells, those distal 36–40 μm high; spores 46–56 μm in longer diameter.

Additional collections: COSTA RICA: **Cartago:** Santa Clara de Cartago, 1950 m, *Maxon & Harvey 8201* (US). **Heredia:** Near Laguna Danta, NE slope of Volcán Barva, 2520–2580 m, *Grayum et al. 7411* (MO); Alto del Roble, 11 k NNE of Heredia, 2100 m, *Lellinger 1062* (US). PANAMA: **Chiriquí:** Between Alto de las Palmas and Cerro de la Horqueta, 2100–2268 m, *Maxon 5509* (US).

The five known collections are from Costa Rica and Panama. Of these, three specify a trunk epiphyte. The species apparently occurs most commonly at about 2000 m, well within the elevational and geographical ranges of *Z. sectifrons*. Most likely there are some ecological factors separating these related species. From personal observations, *Z. sectifrons* usually grows in moderately exposed situations, such as on isolated trees in otherwise cleared pastures. The larger, thinner lamina of *Z. cornuta* suggests a more enclosed, darker habitat.

5. **Zygophlebia eminens** (C. Morton) L. E. Bishop, comb. nov.—*Grammitis eminens* C. Morton, Contr. U.S. Natl. Herb. 38:99, pl. 2. 1967.—TYPE: Ecuador, Pcia. Azuay, Páramo del Castillo, ca. 6–8 km NNE of Sevilla de Oro, 10,000–11,200 ft, *Camp E-5169* (NY).

Epiphyte of moderate size; rhizome rather stout, with brown scales up to 5 × 0.6 m; frond probably pendent, flexed at base of lamina; stipe medium brown, nearly as long or longer than the lamina, 10–20 cm × 1.0–1.5 mm, when young well provided with short, clavate, simple or branched hairs throughout its length, and also with dark brown setae 1.5–2.5 mm long, densely so at the base, very sparsely so distally, the whole stipe usually glabrate with age; rachis wholly embedded in laminar tissue, broadly prominulous, with some small, simple hairs and a few dark brown, widely scattered setae associated with it at least on the dorsal side, but these trichomes often lost with age; lamina subcoriaceous, ovate, broadly lanceolate, or elliptic-oblong, deeply pinnatifid to within 1–3 mm of the rachis, 13–20 × 5–7 cm, narrowed through 1–3 pairs of basal pinnae, at the apex apparently either abruptly truncate or shortly prolonged into a terminal segment; pinnae linear-triangular, up to 50 mm long, 4–8 mm wide, approximate or separated by less than their width, set at 50–60° to the rachis, at base at times expanded basiscopically, distally straight or else noticeably falcate, essentially glabrous though with a few small, simple, clavate-glandular hairs (these most evident when young), with the costa weakly prominulous on either side; veins mostly free, but with many of the veinlets distally furcate, at times connivent with the next distal veinlet; stomata 60–70 × 54–62 μm; sori mostly subimpressed, some superficial, generally inframedial, up to 12 pairs per segment, borne to near the rachis, the pinnae often with a prolonged sterile distal portion; capsules 250–275 × 190–210 μm, with 13–15 annulus cells, the distal ones 37–42 μm high; spores 50–60 μm in longer diameter.

Additional collection: ECUADOR: **Azuay:** Páramo del Castillo, near the lake, trail between Sevilla do Oro and Mendez, 9000–11,000 ft, *Camp E-5102* (US, NY not seen *fide* Morton).

The US paratype is a smaller, sterile plant, quite different in aspect because of the narrow fronds with short, broadly rounded pinnae. The pinnae of the fertile holotype are characteristically (I assume) distally long acuminate.

With its esetose lamina and slightly immersed sori that are fundamentally basal on the segments, *Z. eminens* is clearly part of the *Z. sectifrons* group. Despite the superficial similarity of the fronds to *Z. cornuta*, the scales are similar in size, color, and shape of the cells to those of *Z. dudleyi*. Also, *Z. eminens* and *Z. dudleyi* have widely scattered setae on the rachis. Both *Z. sectifrons* and *Z. cornuta* lack such setae. I believe such characters to be of more importance in elucidating relationships than those of laminar dissection.

6. **Zygophlebia dudleyi** L. E. Bishop, sp. nov. (Fig. 2).—TYPE: Peru, Dept. Cuzco, Pcia. La Convención, Cordillera Vilcabamba, ca. 23 km NE of Hacienda Luisiana and Río Apurimac, pendent epiphyte with sticky leaves, in dense cloud forest, 12°30′S 74°30′W, 3000 m, *Dudley 11144* (NA, isotype US).

Filix epiphytica major pendens quae solum ex altitudine excelsa Andium peruviensium cognoscitur. Rhizoma (unicum mihi adest) validius, paleis ochrobrunneis lineari-triangularibus 4–7 × 0.4–0.8 mm basi truncatis apice

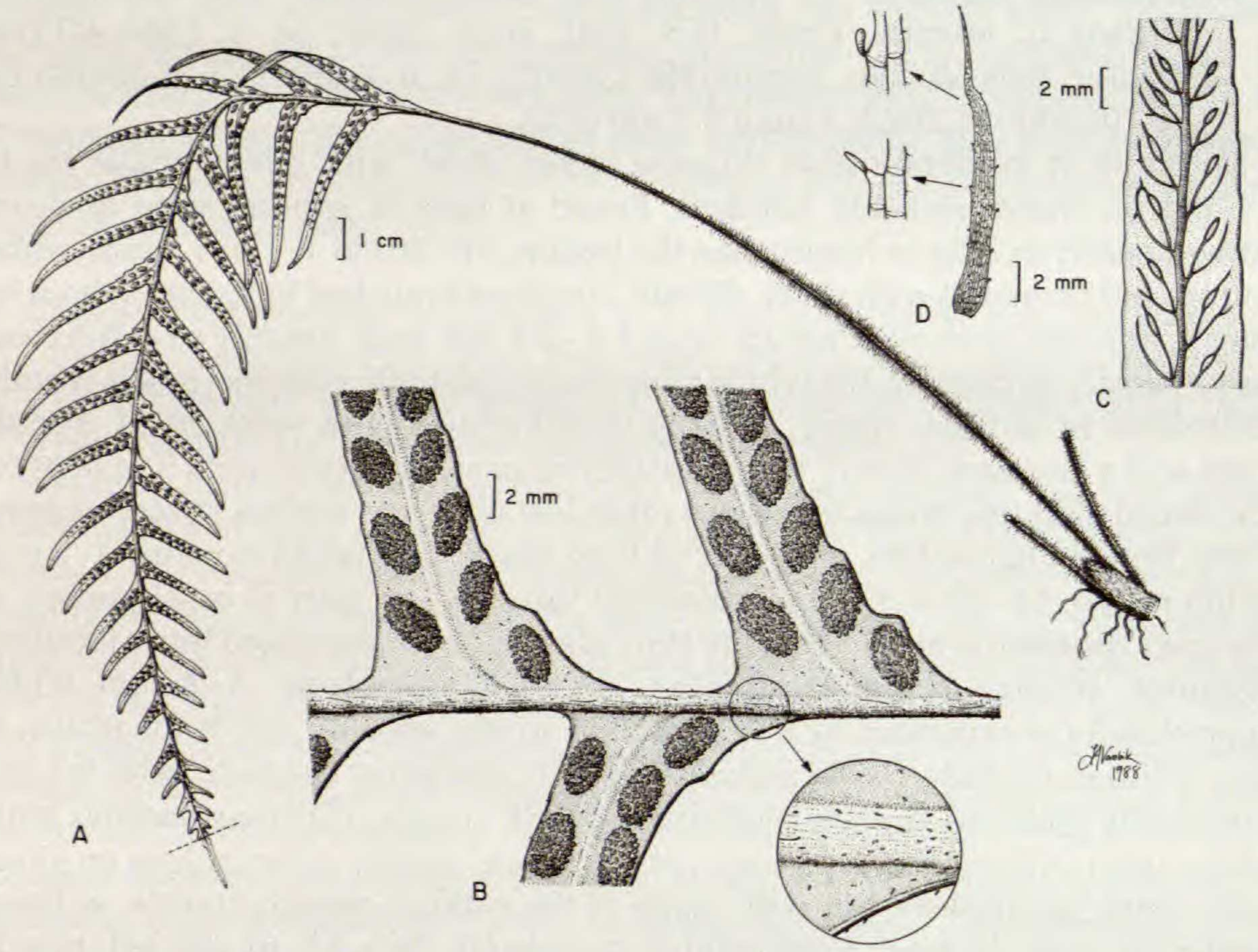

FIG. 2. *Zygophlebia dudleyi* L. E. Bishop, *Dudley 11144*. A. Plant habit. B. Frond detail showing sori and rachis hairs and setae. C. Pinna detail showing venation. D. Rhizome scale showing marginal glands.

acuminatis interdum in caudam productis margine irregulatim integris cellulis obpyriformibus disperse praeditis, cellulis medialibus plerumque 150–200 × 50–80 μm. Frondium sunt stipites brunnei subnitentes pilis glandulosis pluribus pilosi per dimidium basalem setis densis ferrugineis 2.0–4.5 mm his distaliter dissitis ubi veteriores aliquando glabrescentes 1.2–2.0 mm lati × 20–30 cm longi, rhachides utrinque prominentes brunneae vel in laminae texturam immersae pilis glandulosis plerumque simplicibus setis castaneis displicatis (his paucioribus ventraliter) praeditae, laminae ut traditur viscidae anguste triangulares perpinnatae vel profunde pinnatifidae 12–30 cm longae basi vix aut haud angustatae apicibus speciminum mihi non perfectis, pinnis ut videtur interdum reflexis lineari-triangularibus inter se plus quam suis latitudinibus disjunctis hic illic falcatis sub angulo 30–60° a rhachide abeuntibus ad 75 mm longis 3–5 mm latis basi basiscopice decurrentibus acroscopice rectis vel paulo surcurrentibus apice ipso anguste rotundatis in pagina pilos simplices aut furcatos glandulosos ventraliter marginaliterque uberius ferentibus costa utrinsecus prominula, venis saepe liberis sed nonnunquam venulis varie et irregulatim conniventibus, stomatibus 72–85 × 70–80 μm. Quaeque pinna sororum subimpressorum usque ad 28 paria sub maturitate facile marginem attengentia, capsulis maximam partem

obpyriformibus 240–280 × 160–200 μm annulis ex 14–17 cellulis constantibus illis cellulis distalibus 34–40 μm altis sporis hemisphaericis vel subtetraedricis 44–52 μm in diametro longiore ad basin at plerumque ad apicem medialiter vel inframedialiter fert.

Collectori T. R. Dudley diligentiae in illa regione remota in qua legebat causa hanc speciem mirabilem dedo.

Paratype: PERU: **Cuzco:** 28 km NE of Hacienda Luisiana and Río Apurimac, common epiphyte on *Polylepis* at summit ridges, 12°30′S 73°30′W, 3400 m, *Dudley 11218* (NA, US).

This large, striking species can be separated from other species of *Zygophlebia* by the scattered setae on the rachis in combination with the estose pinnae that are strongly angled distad and separated by more than their width. The subimpressed, fundamentally basal sori clearly ally it to the *Z. sectifrons* group, while the lighter brown, smaller scales, the setiferous rachis, and the irregularly free venation seem to bring it closest to *Z. eminens*.

7. **Zygophlebia werffii** L. E. Bishop, sp. nov. (Fig. 3).—TYPE: Peru, Dpto. Pasco, border Pcias. Oxapampa and Pasco; in dwarf forest with *Sphagnum* layer below, in peat layer, 2700 m, *van der Werff et al. 8570* (UC, isotype MO).

Filix robusta erecta quae in tegete bryophytorum terrestrium sub arboribus sylvae nubilae floret. Rhizoma simplex aut ramosum caespitosumque, paleis spadiceis anguste lanceolatis vel triangularibus basi truncatis vel subcordatis apice longe acuminatis 4–10 × 0.4–0.7 mm margine ciliatis pilis hyalinis saltemve pallidioribus, cellulis medialibus 130–200 × 40–60 μm. Frondium sunt stipites erecti nigrofusci subnitentes pilis clavatis parvis simplicibus ramosisve per longitudinem dissitis setulis 0.1–0.6 mm ad basin exceptum dense instructi 0.8–2.0 mm lati 5–20 cm longi, rhachides prominentes sclerenchymate suo per dimidium basalem utrinque exposito setulis illis stipitum similibus copiose praediti, laminae lineari-oblongae perpinnatae vel profunde pinnatifidae 15–25 cm longae basi aliquando aliquanto angustatae apice segmentum apicale distinctum ferentes pinnis linearibus vel linear-triangularibus sub angulo ca. 90° a rhachide abeuntibus ad 30 mm longis 2.5–4 mm latis basi basiscopice aliquanto decurrentibus acroscopice rectis vel paulo constrictis apice parte distali acuminata breviter rotundata in margine pilis clavatis 1–4-furcatis interdum etiam aliquot setis instructi in pagina ventrali pilos parvos dissitos gerentibus costa subimpressa sclerenchymate suo exposito per occasionem setas hic inveniri dorsaliter glabris aut pilis costam prominulam secus, venis areolatis venulis sterilibus venam intramarginalem efficere convenientibus, stomatibus 48–56 × 40–45 μm. Sororum usque ad 12 paria, his fere ad basin gestis at ad apicem carentibus, sub maturitate marginem attengentium, capsulis late ellipsoidis vel obpyriformibus 200–220 × 175–200 μm annulis ex 13–16 cellulis constantibus illis cellulis distalibus 34–40 μm altis sporis hemisphaericis vel subtetraedricis 38–48 μm in diametro longiore quaeque pinna superficialiter medialiterque instruitur.

Collectoris acri atque feracis Henk van der Werff honoris causa filicem propriam nomino.

Paratype: PERU: **Cuzco:** Villcabamba, Hacienda on Río Chinchao, on clay bank, ca. 6000 ft, *Macbride 5145* (F).

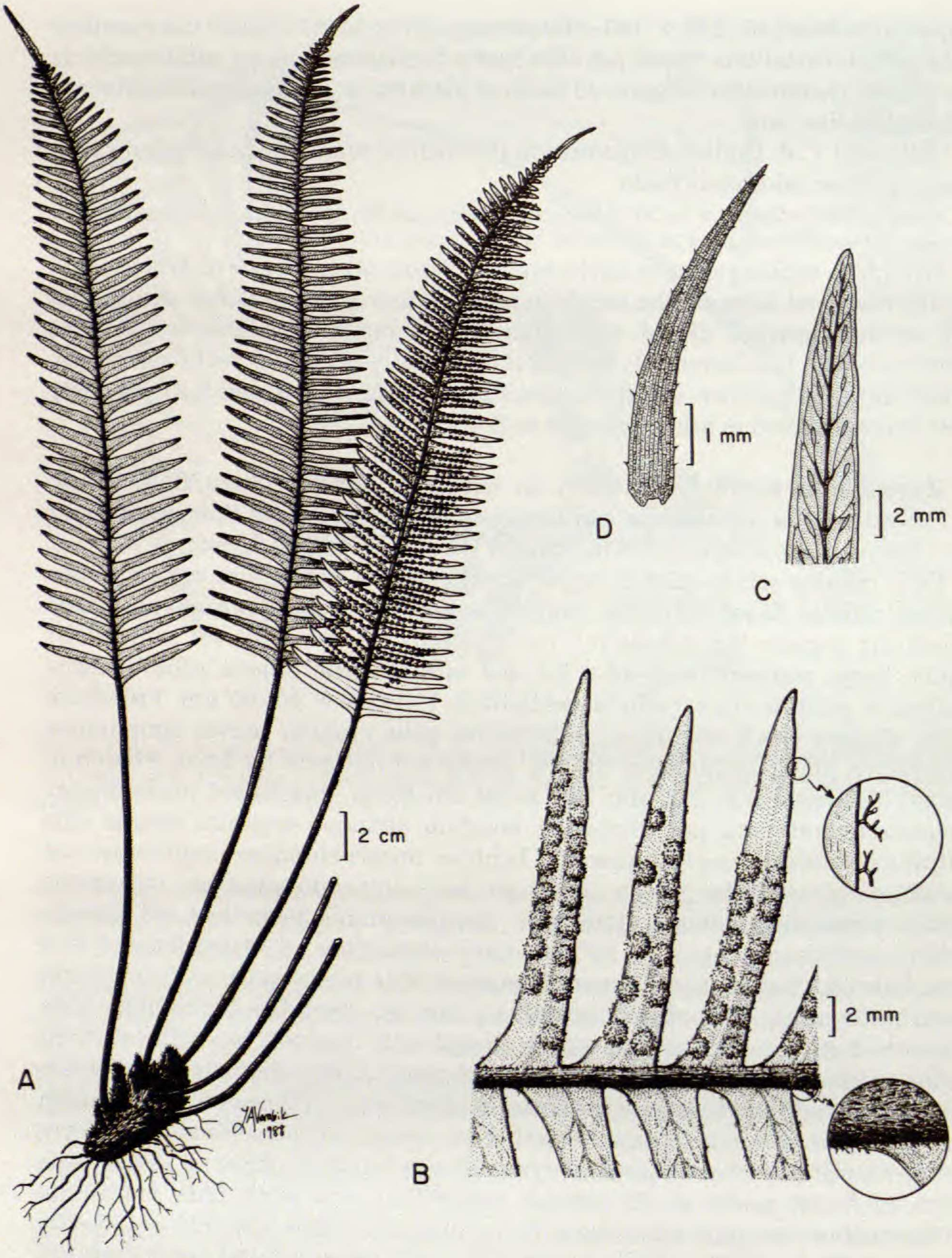

FIG. 3. *Zygophlebia werffii* L. E. Bishop, *van der Werff et al. 8570*. A. Plant habit. B. Frond detail showing hairs and setulae. C. Pinna detail showing venation. D. Rhizome scale.

This is the only species of the genus that is not fundamentally a pendent epiphyte. The erect fronds with robust stipes and rachides appear correlative to this fact. It seems not closely related to any other member of the genus. The lack of laminar setae and the basally borne sori set it apart from *Z. mathewsii* and *Z. longipilosa*. The superficial sori and the numerous small setae on the rachis separate it from the *Z. sectifrons* group.

Zygophlebia werffii is immediately to be recognized from its congeners by the stout, black stipe and rachis densely provided with short setae. But more than any other member of its genus, it is likely to be mistaken for a *Ceradenia*. From all species of that genus it is easily distinguished by its erect, completely pinnate fronds with net-veined, closely spaced, narrow pinnae.

The genus *Zygophlebia* also occurs in Africa. Through the kindness of Dr. Barbara Parris at Kew I have been able to examine the appropriate types, but this material is very sparse. The types of *Polypodium villosissimum* Hook., *P. forsythianum* Baker, and *P. subpinnatum* Baker all pertain to this genus. *Polypodium villosissimum* and *P. forsythianum* are very likely conspecific, as has been suggested by Tardieu-Blot (in Humbert, 1960). The types of these are similar in having rather thin laminae, lighter brown stipes and scales, and pinnae which are mostly oblong and clearly angled to the rachis. *Polypodium forsythianum* differs only in its smaller size. *Polypodium subpinnatum* likely differs from these, possibly on the species level, although it has been accorded subspecific rank by Schelpe (1969). This plant has darker brown stipes and rhizome scales, larger laminae which are broadest at the middle and more sharply reduced toward the base, relatively shorter stipes, more regularly subimpressed sori, and pinnae widest at the base and more broadly angled to the rachis.

A plant I believe probably to represent a species distinct from all these was described as *Polypodium villosissimum* var. *majus* by Reimers (in Mildbraed, 1933). Although I have not examined this type, there is a specimen at UC (*Schlieben 3017*) from the same collection locality that matches the type description. This sheet differs conspicuously from all the types here discussed by its much thicker laminae and more robust, wider stipes. The cells of the rhizomes scales are mostly 1–1.5 times as long as broad and have walls more than 20 μm thick. The scales of the types just discussed have cells 3–6 times as long as broad and intercellular walls 10–15 μm wide.

It is clear that the African species of *Zygophlebia* merit closer examination than the few specimens I have been able to study. Therefore, I elect to transfer only the oldest name until more and better specimens can be inspected:

Zygophlebia villosissima (Hook.) L. E. Bishop, comb. nov.—*Polypodium villosissimum* Hook., Sp. fil. 4:197. 1862.—*Grammitis villosissima* (Hook.) Ching, Bull. Fan Mem. Inst. Biol., Bot. 10:241. 1941.—*Ctenopteris villosissima* (Hook.) Harley, Contr. Gray Herb. 177:92. 1955.—*Xiphopteris villosissima* (Hook.) Alston, Bol. Soc. Brot., ser. 2. 30:27. 1956.—LECTOTYPE: Sierra Leone, Sugar-loaf Mts., *Barter s.n.* (K), by Schelpe, Contr. Bolus Herb. 1:8. 1969.

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